Insect Transmission of Tomato Yellow Leaf Curl Viruses

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ABSTRACT

Whitefly-transmitted tomato yellow leaf curl disease (TYLCD) is associated with many phylogenetically related viruses named tomato yellow leaf curl viruses that belong to the genus *Begomovirus* of the family *Geminiviridae*. Begomoviruses are mainly transmitted by the sweet potato whitefly, *Bemisia tabaci* (family Aleyrodidae, order Hemiptera), which is also a species complex with many biotypes. TYLCD is one of the most devastating viral diseases affecting tomato production in tropical and temperate areas worldwide, and the invasion of begomoviruses into a new region always accompanies the expansion of *B. tabaci* population. It is always thought that *B. tabaci* transmits begomoviruses in a persistent-circulative transmission mode; however, some studies showed that begomoviruses not only circulate in the hemolymph of *B. tabaci* but also replicate in it. In addition, *Tomato yellow leaf curl virus* Israel isolate (TYLCV-Is) was reported to be transovarially transmitted from virus-infected females to their progeny. TYLCV-Is is a well-studied begomovirus, and its transmission by *B. tabaci* has been examined in details. The acquisition access period and inoculation access period of TYLCV-Is transmission seems to be much shorter than those characteristics of typical persistent-circulative transmission mode. The vector transmission of TYLCV-Is requires a short latent period, and the virus persists and replicates in its insect vector. After reviewing related studies, we propose that few begomoviruses (at lease TYLCV-Is) are transmitted by *B. tabaci* in a special type of persistent-propagative transmission mode. More studies on the vector transmission of other begomoviruses are needed.

Keywords: *Begomovirus, Bemisia tabaci*, transmission mode, transovarial transmission, insect vector

INTRODUCTION

The feeding of sap-sucking insects always accompanies the transmission of plant viruses, and the feeding damage and viral disease cause great economic loss [40]. Many viral diseases of tomato are transmitted by the sweet potato whitefly, *Bemisia tabaci*, and the diseases often cause yield loss of tomato. *Bemisia tabaci*, an insect vector, transmits more than 111 virus species that induce disease symptoms, e.g. mosaic, yellowing, leaf curling, crinkling and even stunting on plants (Fig. 1) [45].

Among several plant diseases transmitted by *B. tabaci*, tomato yellow leaf curl disease is one of the most devastating viral diseases affecting tomato production in tropical and temperate areas worldwide [39, 57]. Tomato yellow leaf curl disease is associated with many phylogenetically related viruses named tomato yellow leaf curl viruses that belong to the genus *Begomovirus* of the family *Geminiviridae* [47]. Evidence shows that the invasion of begomoviruses into a new region always accompanies the expansion of *B. tabaci* population [6, 15, 24]. In Spain, the displacement between two species of tomato yellow leaf curl viruses has been reported [79], so as two tomato begomoviruses in Taiwan [85]. The displacement of tomato begomoviruses in the fields may be due to the invasion of new virus/vector and the different transmission efficiency of these viruses by their insect vectors [79, 85].

It is always thought that *B. tabaci* transmits begomoviruses in a persistent-circulative transmission mode [26, 40]. It means that begomoviruses infect *B. tabaci* and disseminate from alimentary gut to salivary glands without virus replication. However, some studies showed that begomoviruses not only circulate in the hemolymph of *B. tabaci* but also replicate in it [25, 33, 54]. The relationships between the virus, host plant, and whitefly vector are intricate [38, 66]. Whether the persistent transmission of begomoviruses by whiteflies is propagative or circulative is still controversial. We reviewed studies related to the transmission of various begomoviruses by *B. tabaci* and discussed the transmission mode of these begomoviruses.

Bemisia tabaci

Bemisia tabaci belongs to the family Aleyrodidae of the order Hemiptera. Among more than 1,550 species in the family Aleyrodidae, *B. tabaci* is considered to be the most important agricultural pest [13, 27]. *Bemisia tabaci* has high genetic variation within species with a number of recognized biotypes. Over the past decades, the application of molecular markers has distinguished more than 20 biotypes of *B. tabaci* [48, 70].

These biotypes differ in biological characteristics such as host range, virus transmission ability, insecticide resistance, and endosymbionts [3, 13, 41, 80, 90]. Some taxonomists even define *B. tabaci* as a species complex containing at least 28 morphologically indistinguishable species [28, 51].

Within this whitefly complex, B biotype and Q biotype have risen to international prominence [13, 28]. Recently, the spread of *B. tabaci* in greenhouses in temperate areas has been reported [41, 60, 88]. Most of these invasive whiteflies were identified as B biotype of *B. tabaci* that has spread to the areas in America, Africa, Asia, and Australia [9, 28]. Since 1980s, invasive B biotype has risen in status to one of the most damaging pests of crops worldwide [13, 14, 75], and it is currently listed as one of the top 100 invasive species worldwide [13]. Liu et al. [50] further proposed that the asymmetric mating interactions between closely related groups of *B. tabaci* is a driving force contributing to the invasion and displacement of invasive B biotype. In addition, Q biotype of *B. tabaci* has recently become a new invader via the same pathway as B biotype [27, 43].

In recent years, Q biotype of *B. tabaci* has invaded to many countries in Asia, Australia, and America, and caused economic loses of many cash crops [22, 53, 92]. There are four biotypes of *B. tabaci* reported in Taiwan, and invasive B biotype has out-competed endemic Nauru and An biotypes [44]. Q biotype of *B. tabaci* was also found in poinsettia greenhouses, but no field population was found in Taiwan [43].

Bemisia tabaci is a tiny insect (mostly 0.8 mm in length) with high reproductive rate and many generations in a year. The life history of *B. tabaci* is divided into 3 stages: egg, nymph, and adult (Fig. 2). The eggs are pyriform and laid in groups. First instar nymphs, commonly called crawlers, are flat in body shape. The mobile crawlers walk to find a suitable area on the leaf and stay at the same feeding site through whole nymphal stage. Second and third instar nymphs become stationary without any legs. Fourth instar nymphs, also referred to as red-eyes nymphs, turn yellowish in body color and thickening of body shape. Late in fourth instar stage, they stop feeding and subsequently molt to adult. The body of the adult is yellowish and has four membranous wings. The fore legs and hind legs of the adult distribute wax powder over the wings and the rest of body. In general, it takes 20-30 days to develop from eggs to adults in the warm climate and 30-45 days in the cool climate [17]. The lifespan of the adult is 25 to 30 days. There are 8-12 generations of *B. tabaci* in a year, and an adult female can laid up to 300 eggs in her lifespan.

Bemisia tabaci is a phloem-feeding insect and mostly feeds on herbaceous species,

which can result in greater than 50% yield reduction through sap sucking [17]. Plant host range of *B. tabaci* includes *Brassica* spp., tomatoes, eggplants, squash, cucumber, beans, cotton, and poinsettia. *Bemisia tabaci* affects crops with its feeding in three ways: 1) removing plant sap and subsequently reducing the plant vigor and yields, 2) excreting honeydew that fosters sooty mold fungi, and 3) transmitting plant viruses. *Bemisia tabaci* is known to transmit 111 plant virus species including many species of begomoviruses [45].

Begomovirus

Four genera in the family *Geminiviridae* have been established: *Mastrevirus*, *Curtovirus*, *Topocuvirus*, and *Begomovirus* [47]. *Begomovirus* is mainly transmitted by *B. tabaci* [15]. Whereas *Mastrevirus* and *Curtovirus* are transmitted by leafhoppers, *Topocuvirus* is transmitted by a treehopper *Micrutalis malleifera* [5, 10, 76]. The genus *Begomovirus* currently includes about 200 formally accepted virus species, and it is the largest genus in the family *Geminiviridae* [64]. Begomoviruses have a very wide host range but are limited to the dicotyledonous plants. The viruses cause a lot of economic damages to important crops such as tomatoes, beans, squash, cassava, and cotton in the world [12, 24, 84]. Begomoviruses are mostly restricted to the phloem of plants and induce disease symptoms, e.g. mosaic, yellowing, leaf curling, crinkling, and even stunting on plants [45]. Tomato yellow leaf curl disease is the most devastating disease caused by begomoviruses that affects tomato crops in tropical and temperate areas worldwide [29, 49, 57].

Members in the family *Geminiviridae* have circular single-strand DNA (ssDNA) genomes, and their virus particles consist of characteristic two incomplete icosahedra joined together [47]. The genome of geminivirus contains six open reading frames (ORFs). According to genome organization, begomoviruses are divided into two groups, monopartite viruses and bipartite viruses. Monopartite begomoviruses contain only one DNA segment (referred to as DNA-A) with genome size at 2.5-2.7 kb; bipartite begomoviruses contain two DNA segments (referred to as DNA-A and DNA-B) with similar genome size (2.5-2.7 kb) [64]. Some species of *Begomovirus* are associated with DNA satellites [65].

Among six ORFs of monopartite begomoviruses, the viral sense V1 gene encodes coat protein (CP), which is the only structural protein of begomovirus particles and is related to virus movement and vector transmission [83]; V2 gene encodes movement

protein; the complementary sense C1, C2, C3, and C4 genes encode replication associated protein, transcriptional activator protein, replication enhancer protein, and RNA silencing suppressor, respectively [31]. In bipartite begomoviruses, there are six ORFs in DNA-A: the viral sense AV1 and AV2 genes encode the CP and silencing suppressor, respectively [31, 37, 59]; four ORFs in the complementary sense, AC1, AC2, AC3, and AC4 genes, encode the same functional proteins as C1, C2, C3, and C4 genes of monopartite begomoviruses [31]. DNA-B contains two ORFs; the viral sense BV1 gene and the complementary sense BC1 gene encode nuclear shuttle protein and movement protein, respectively [31].

Over the past decades, diseases caused by begomoviruses have emerged as serious diseases to the cultivation of a variety of vegetable crops [16]. The host plants of begomoviruses range from more than 10 families of crops to weeds. Weeds serve as reservoirs of begomoviruses, so they play an important role in the emergence of viral diseases of crops [7, 11, 32, 46]. In addition, anthropogenic activity is a key factor of long-distance dispersal of plant viruses. A well-documented case showed that *Tomato yellow leaf curl virus* (TYLCV), a begomovirus, introduced into the Dominican Republic from Israel in 1992 [71, 73].

In Taiwan, there are at least six begomovirus species occurring in the fields including *Ageratum yellow vein Taiwan virus*, *Poinsettia leaf curl virus*, *Sweet potato leaf curl virus*, *Tomato leaf curl Taiwan virus* (ToLCTWV), *Tomato yellow leaf curl Thailand virus* (TYLCTHV), and *Tomato leaf curl Hsinchu virus* [45, 85], and the viruses are transmitted mainly by *B. tabaci*. In the fields, crops are usually infected with more than one species of begomoviruses, and the predominant species belong to tomato yellow leaf curl virus complex [64, 85].

Transmission biology of tomato yellow leaf curl viruses

Insects transmit the majority of described plant viruses. There are more than 1,000 plant viruses proved to be transmitted by insect vectors [40]. Hemipteran insects transmit most insect-borne plant viruses via piercing-sucking mouthparts. The food canal of hemipteran insects is formed by the opposed maxillae held together by a system of grooves, and the maxillae also contain the salivary canal [21]. Plant-feeding hemipteran insects are specialized as phloem, xylem, or mesophyll feeders [21]. Most plant viruses would infect phloem tissues so phloem-feeding hemipteran insects are the main vectors of these plant viruses. Insects transmit plant viruses in three transmission

modes: 1) nonpersistent, 2) semipersistent, and 3) persistent transmission [63]. Depending on the multiplication of virus in its insect vector, persistent transmission is further divided into two types: persistent-circulative and persistent-propagative [63](Table 1).

Bemisia tabaci is a principal insect vector of begomoviruses. *Bemisia tabaci* acquires begomovirus when it feeds the phloem sap and transmits the virus when it feeds on a new susceptible host, thus vectors are often the species that colonize the host plant. *Tomato yellow leaf curl virus* Israel isolate (subsequently referred to as 'TYLCV-Is') is a well-studied begomovirus, and its transmission by *B. tabaci* has been examined in details [33, 34, 78]. It is always thought that *B. tabaci* transmits begomoviruses in a persistent-circulative transmission mode [40], but it still remains a controversial issue. Interestingly, TYLCV-Is was documented to be transmitted from mother to offspring, and the offspring remain infective (i.e. transovarial transmission) [33], and some studies suggested that the virus could replicate in its insect vector [25, 54]. It is necessary to verify the transmission mode of begomoviruses by *B. tabaci*.

Vector transmission of geminiviruses is in a persistent-circulative mode [40]. *Cicadulina mbila*, a leafhopper, transmitted *Maize streak virus* (genus *Mastrevirus*) with an acquisition access period (AAP) of 3 h, and the virus was retained in its insect vector for 35 days [2, 40]. *Circulifer tenellus*, a leafhopper, transmitted *Beet curly top virus* (genus *Curtovirus*) with an AAP of 1 h, but the inoculation access period (IAP) was as long as 5 days for successful transmission of the virus, and the retention time of the virus was 30 days [82]. *Tomato pseudo-curly top virus* was transmitted by *Micrutalis malleifera,* a treehopper, with an AAP of 24 h, and the latent period of the virus transmission was as long as a week [81].

Most persistent-circulatively transmitted viruses require a period of hours to days for successfully acquiring and inoculating viruses. Interestingly, *B. tabaci* transmits begomoviruses with shorter AAP and IAP than the viruses belonging to other genera of *Geminiviridae* (Table 1). TYLCV-Is was detected in 15% of *B. tabaci* after they were fed on virus-infected plants for 30 min, and the frequency of the virus detection increased with the duration of the AAP [91]. The minimum IAP of TYLCV-Is was 15-30 min, and viral DNA was only detected in 10% of test plants [52]. Atzmon et al. [4] also reported that TYLCV-Is was detected in all test plants with an IAP of 30 min after an AAP of 24 h. The similar value of a minimum AAP of 1 h was reported for another begomovirus *Tomato yellow leaf curl Sardinia virus* (TYLCSV)[18]. The same experiment

also conducted with *Squash leaf curl virus* (SLCV), a begomoviruses, and the minimum AAP and IAP were 12 h and 24 h, respectively [72]. According to our unpublished results, *B. tabaci* successfully acquired and inoculated TYLCTHV and ToLCTWV within a couple of hours. In summary, the AAP and IAP of vector transmission of most begomoviruses by *B. tabaci* seem to be much shorter than those characteristics of typical persistent-circulative transmission mode (Table 1).

The other two transmission characteristics, i.e. latent period and retention time, are employed to distinguish persistent transmission mode and non-persistent transmission mode. A latent period is required when virus particles circulate or multiply in insect vector's body until they are ready to be inoculated to a new susceptible host. Most studies proved that TYLCV-Is lurks in *B. tabaci* with a short latent period. Once *B. tabaci* acquired TYLCV-Is, it kept the virus and remained infective through its entire life (~30 days) [25]. The latent period of TYLCV-Is was reported to be 20-24 h [23] or 8 h [35]. The latent period of SLCV and *Tomato leaf curl virus* (ToLCV), two begomoviruses, were 8 h and 6 h, respectively, which were similar with that of TYLCV-Is. [25, 58, 77]. Rubinstein and Czosnek [78] verified the ability of viruliferous *B. tabaci* to transmit TYLCV-Is to tomato plants steadily decreased with age but did not disappear completely until they died. Another study showed that TYLCSV DNA was remained in *B. tabaci* up to 22 days after the end of AAP, but the infectivity of the whiteflies only persisted till 18 days [19]. We also found that TYLCTHV and ToLCTWV needed a short latent period to be transmitted and viruliferous *B. tabaci* kept infective through adulthood (Weng and Tsai, unpublished results). In summary, the transmission of most begomoviruses by *B. tabaci* requires a short latent period, and the viruses persist in their insect vector lifelong. The latent period and retention time of begomoviruses fit the transmission characteristics of persistent-circulative and persistent-propagative transmission modes, respectively (Table 1).

The replication of begomoviruses in *B. taabci* has been examined by several research groups. Czosnek et al. [25] reported that TYLCV-Is DNA was detected by Southern blot hybridization in viruliferous *B. tabaci* after a 1 h-AAP, and the amount of viral DNA steadily increased after a lag period of 8 h and reached maximum level 16 h after and decreased thereafter. In another study, TYLCV Egypt isolate multiplied in *B. tabaci* starting from the end of 12 h-AAP to 108 h, and the virus titer stayed in a stable level from 108 to 180 h [54]. Following the acquisition of TYLCSV,

accumulation of viral DNA was not observed after an AAP of 12 h [19]. Therefore, the propagation of begomoviruses in their insect vector remains a controversial issue.

Many studies have been focused on the expression of viral genes in *B. tabaci* after feeding on begomovirus-infected plants [1, 36, 56, 68, 80] Vial gene expression indirectly implies the replication of begomoviruses in their insect vector. Real-time RT-PCR assay proved that the transcripts of V1, V2, and C3 genes of TYLCV-Is increased after feeding on virus-infected plants and then transferred to nonhost plants, but the transcripts of AV1, BC1, and BV1 genes of *Tomato mottle virus* (ToMoV) rapidly became undetectable [80]. The transcripts of TYLCV-Is C2 gene in the B and Q biotypes of *B. tabaci* increased along with the feeding periods of 6-72 h on virus-infected tomato plants [68]. The transcripts of TYLCV-Is V1 gene were localized in filter chamber and descending midgut of *B. tabaci* [36]. In summary, virus replication or viral gene transcription are proved in some begomoviruses (e.g. TYLCV-Is), but other begomoviruses do not replicate in their insect vector (e.g. ToMoV). The replication of TYLCV-Is in *B. tabaci* fits the transmission characteristics of persistent-propagative transmission mode (Table 1).

Infection and dissemination of begomoviruses in *Bemisia tabaci*

The infection and dissemination of begomoviruses in *B. tabaci* were mostly studied with TYLCV-Is and TYLCSV. The infection of tissues and organs of viruliferous *B. tabaci* was examined by immunohistological methods using antibodies raised against the CP of begomoviruses. TYLCV-Is was immunolocalized to descending midgut, filter chamber, and primary salivary glands [15, 26]. TYLCV Kisozaki isolate [87], which is closely related to TYLCV-Is, also infected the caecum of midgut, filter chamber, and ascending/descending midgut of *B. tabaci* [67]. Uchibori et al. [86] also verified TYLCV-Is overcame with the barriers of midgut and salivary gland by the way of interacting with vesicle-like structures and accumulating in the epithelial cells of descending and ascending midgut of *B. tabaci*. TYLCSV also showed the similar infection status as TYLCV-Is; the virus was detected in midgut microvilli and primary salivary glands [20, 55]. Although viral DNA fragments have been amplified from ovary tissue of *B. tabaci* that acquired TYLCV-Is via feeding on virus-infected plants [33], no specific labeling of the CP by immunohistology in ovaries was observed [20]. SLCV was reported to infect a number of organs and tissues of *B. tabaci* including midgut and salivary glands [69]. ToMoV and *Cabbage leaf curl virus*, two

begomoviruses, were also detected in salivary glands of viruliferous *B. tabaci* [55].

The dissemination of begomoviruses in viruliferous *B. tabaci* has been studied by PCR assay for TYLCV-Is and SLCV. TYLCV-Is DNA was firstly detected by PCR in the head of *B. tabaci* 10 min after the end of AAP, in the midgut 40 min after, in the hemolymph 90 min after, and in the salivary glands 5.5 hours after [35]. In another study, SLCV was firstly detected in the hemolymph of *B. tabaci* 2 h after the end of AAP, and in the saliva and honeydew 8 h after [77]. More studies focusing on the dissemination of begomoviruses in viruliferous *B. tabaci* are expected.

Transovarial transmission

Transovarial transmission is important in plant disease epidemiology. When viruliferous insect vectors pass virus from mother to their progeny, the progeny are ready to transmit the virus without virus acquisition and latent period. Transovarial transmission has been reported in many insect borne plant viruses [30, 42, 61, 62]. It is important to clarify whether transovarial transmission occurs in tomato yellow leaf curl viruses because it would affect the prediction of disease epidemiology.

Most studies showed that tomato yellow leaf curl viruses could be vertically passed from mother to their offspring (i.e. transovarial passage) (Table 2), but only Ghanim et al. [33] documented that TYLCV-Is not only transovarially passed to the offspring of viruliferous *B. tabaci* but also was ready to be transmitted to new susceptible plants by the whitefly offspring. However, TYLCSV was only passed to the offspring of viruliferous *B. tabaci*, but the offspring did not retain the infectivity [8]. The transovarial transmission of two TYLCV isolates, which are closely related to TYLCV-Is was also examined; the whitefly offsprings inherited the virus from their mothers, but the offsprings did not retain the ability to transmit the virus [8, 68]. The transovarial transmission of TYLCV-Is and *Tomato yellow leaf curl China virus* (TYLCCNV) by the B and Q biotypes of viruliferous *B. tabaci* has also been examined. The results showed that small proportion of the offspring inherited the viruses, but none of them kept the virus until adulthood except that 3% of Q biotype adult retained TYLCV-Is [89]. Apparently, the transovarial transmission was only observed in TYLCV-Is but not in other species of begomoviruses [8, 67, 74]. We also examined the transovarial transmission of TYLCTHV and ToLCTWV that are predominant begomoviruses in Taiwan. TYLCTHV could be transovarially passed to a small proportion of progeny of viruliferous *B. tabaci*, and the progeny were still infective

(Wang and Tsai, unpublished results). However, ToLCTWV could not be passed from the mother to the progeny, and the transovarial transmission did not occur for the virus. In summary, transovarial transmission only occurs in some begomoviruses (e.g. TYLCV-Is and TYLCTHV), and most tomato yellow leaf curl viruses examined failed to be transmitted through transovarial transmission.

CONCLUSION

Begomoviruses cause a lot of economic damages to important vegetable crops such as tomatoes and squash in the world [12, 24, 84], and they are mainly transmitted by *B. tabaci* [15]. The invasion of begomoviruses into a new region always accompanies the expansion of *B. tabaci* population [6, 15, 24]. *Bemisia tabaci* is a tiny insect with high reproductive rate and many generations in a year. Both begomoviruses and *B. tabaci* have very wide host ranges. The alliance of begomoviruses and *B. tabaci* poses a threat to the production of important vegetable crops worldwide. The disease induced by tomato yellow leaf curl viruses is the most devastating disease associated with begomoviruses that affects tomato crops in tropical and temperate areas [29, 49, 57].

It is always thought that *B. tabaci* transmits begomoviruses in a persistent-circulative transmission mode [40], but it still remains a controversial issue. TYLCV-Is is a well-studied begomovirus, and its transmission by *B. tabaci* has been examined in details [33, 34, 78]. The AAP and IAP of vector transmission of most begomoviruses (including TYLCV-Is) by *B. tabaci* seem to be much shorter than those characteristics of typical persistent-circulative transmission mode. The transmission of most begomoviruses (including TYLCV-Is) by *B. tabaci* requires a short latent period, and the viruses persist in their insect vector lifelong. The latent period and retention time of begomoviruses fit the transmission characteristics of persistent-circulative and persistent-propagative transmission modes, respectively.

Virus replication or viral gene transcription in insect vector are demonstrated in some begomoviruses (e.g. TYLCV-Is), but other begomoviruses (e.g. ToMoV) do not replicate in their insect vector. The replication of TYLCV-Is in *B. tabaci* fits the transmission characteristics of persistent-propagative transmission mode. Interestingly, the transovarial transmission was only observed in TYLCV-Is and TYLCTHV but not in other species of begomoviruses [8, 67, 74]. According to the abovementioned studies, it seems that few begomoviruses (e.g. TYLCV-Is) are transmitted by *B. tabaci* in a special type of persistent-propagative transmission mode. More studies on the vector

transmission of other begomoviruses are needed.

The interactions between whitefly and begomovirus are intricate. Despite the economic importance of tomato yellow leaf curl disease, little information for the begomovirus-whitefly interaction is known. Many questions remain to be answered such as the replication and transcription of begomoviruses in *B. tabaci*, the transovarial transmission of begomoviruses, and the deleterious effects of begomovirus infection in its insect vector. Lacking information about virus-vector interactions impairs the efficiency of insect-borne disease control because insect vector is the best target for controlling the diseases. Detailed knowledge of the interrelationship between whiteflies and begomoviruses may be able to help us develop novel strategies to protect crops from begomovirus-incited diseases.

ACKNOWLEDGMENTS

This work was supported by grant no. 101AS-10.2.1-BQ-B4 and 102AS-10.2.1-BQ-B5 from Bureau of Animal and Plant Health Inspection and Quarantine, Taiwan, R.O.C.

Fig. 1. Symptoms on tomato (*Lycopersicon esculentum*) caused by tomato yellow leaf curl disease. Leaves of the plant infected with *Tomato yellow leaf cur Thailand virus* exhibited symptoms of mosaic, yellowing, leaf curling, crinkling, and stunting. This photograph was taken in a field in Changhua, Taiwan, in 2010 (Photo by C. W. Tsai, National Taiwan University).

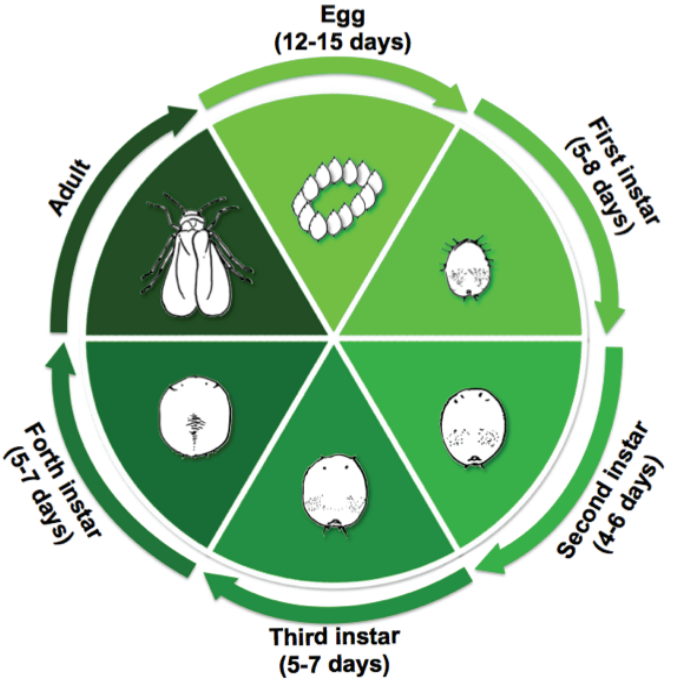

Fig. 2. Graphic representation of the life cycle of *Bemisia tabaci*.

Table 1. Transmission characteristics of *Tomato yellow leaf curl virus* Israel isolate

Transmission characteristics[a]	**Persistent-circulative**[b]	**Persistent-propagative**[b]	**TYLCV-Is**	**References**
Acquisition access period (AAP)	Hours-days	Hours-days	30 min	Zeidan and Czosnek, (1991)
Inoculation access period (IAP)	Hours-days	Hours-days	15-30 min	Mansour and Al-Musa, (1992)
Latent period	Hours-days	Days-weeks	8 h	Gahnim et al. (2001)
Retention time	Days-weeks	Lifelong	Lifelong	Rubinstern and Czosnek, (1997)
Virus multiplication in hemolymph	No	Yes	Yes	Czosnek et al. (2001)
Transovarial transmission	No	Often	Yes	Gahnim et al. (1998)

[a] The definitions of these terms can be found in Nault (1997).
[b] The data of transmission characteristics are derived from Hogenhout et al. (2008).

Table 2. Transovarial passage of tomato yellow leaf curl viruses

Virus	**Biotypes of *Bemisia tabaci***	**Life stage**			**References**
		Egg	**Nymph**	**Adult**	
TYLCV-Is	B	81%	37%	57%	Ghanim et al. (1998)
TYLCV-Is	B	0%	0%	0%	Polston et al. (2001)
TYLCV-Is	B	0%	0%	0%	Bosco et al. (2004)
TYLCSV	B	9%	29%	2%	Bosco et al. (2004)
TYLCV-Is	B	28%	8%	0%	Wang et al. (2010)
TYLCV-Is	Q	17%	15%	3%	Wang et al. (2010)
TYLCCNV	B	19%	11%	0%	Wang et al. (2010)
TYLCCNV	Q	1%	1%	0%	Wang et al. (2010)
TYLCV-Is	B	30%	11%	0%	Pan et al. (2012)
TYLCV-Is	Q	50%	17%	0%	Pan et al. (2012)

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